NeoBiota 65: 71–91 (2021)
doi: 10.3897/neobiota.65.67192
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

Diversity of alien roadside herbs along an elevational gradient in western Mexico

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Academic editor: Brad Murray | Received 10 April 2021 | Accepted 6 May 2021 | Published 28 May 2021

Citation: Pérez-Postigo I, Bendix J, Vibrans H, Cuevas-Guzmán R (2021) Diversity of alien roadside herbs along an elevational gradient in western Mexico. NeoBiota 65: 71–91. https://doi.org/10.3897/neobiota.65.67192

Abstract

Growing numbers of alien plant species threaten natural ecosystems worldwide. Mexico, as a megadiverse country, has lower numbers of alien species than other regions in America. However, there is a lack of information on the factors that determine the diversity patterns of alien species and their relative importance in the vegetation. The diversity of alien roadside herbs was analysed along an elevational gradient in western Mexico, including their relationship with environmental factors. Three hundred and seventeen herbaceous species were found in 37 sampling sites; 10% were aliens. The proportion of alien species in the ruderal herbaceous communities was lower than the average for this vegetation type in the country. Absolute species richness of natives was significantly and positively correlated with elevation. Absolute species richness of aliens was not significantly correlated with elevation, still; higher values were found at lower elevations. Generalised linear models for relative species richness and relative abundance of aliens with elevation had positive estimates near 0, which, though statistically significant, indicated a weak relationship. Other environmental co-factors, such as the distance to roads and highways, climatic variables, and disturbance indicators, were included in a random forest model. No clear correlation patterns were found. This seemingly random distribution of alien herbaceous plants in the region might be caused by the relatively recent introduction of most of the species. They have not yet had time to expand their distribution to their potential maximum. The early stage of the naturalisation process allows us to minimise the further spread of some species with targeted management and prevent them from becoming invasive.

Keywords

Environmental variables, exotic plant species, ruderal weed species, Sierra de Manantlán

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Introduction

Mexico has far fewer alien species of higher plants, in both relative and absolute numbers, than the USA and Canada, Europe or various South American countries (Espinosa-García et al. 2004b; Villaseñor and Espinosa-García 2004; van Kleunen et al. 2015; Espinosa-García and Villaseñor 2017). A recent survey estimated between 700 and 750 species (Espinosa-García and Villaseñor 2017) which is less than 3% of the flora. Most of them are herbaceous weeds and grasses (Espinosa-García et al. 2004a; Villaseñor and Espinosa-García 2004; Espinosa-García and Villaseñor 2017). They are also, with some exceptions, less successful in terms of the size of their distribution area (Espinosa-García et al. 2004b) or dominance in local weed vegetation.

However, Mexico is a mega-diverse country, and it is risky to generalise results derived from individual local or regional projects (Trejo and Dirzo 2002; CONABIO and SEMADET 2017). Publications on alien plant species in Mexico are scarce, scattered and variable (Espinosa-García and Villaseñor 2017; Ramírez-Albores et al. 2019). Some information is available for the whole country, but most results are restricted to central Mexico or the northern states (Espinosa-García et al. 2004a; Villaseñor and Espinosa-García 2004; Ramírez-Albores et al. 2019). A major effort is needed to study the present-day situation at different scales (Espinosa-García 2009; Espinosa-García and Villaseñor 2017).

Ruderal and roadside vegetation is often the most critical dispersal channel for the initial introduction of alien plants. Roads cross different environmental conditions, such as soils and climate (Kowarik and von der Lippe 2007). After expanding along them, the populations may invade the adjacent vegetation (Kowarik and von der Lippe 2007; Pollnac et al. 2012; Otto et al. 2014; Martínez-De La Cruz et al. 2015; McDougall et al. 2018). Although some studies exist on aliens in roadside vegetation (Otto et al. 2014), this type of vegetation is not well-studied in Mexico (Pollnac et al. 2012; Martínez-De La Cruz et al. 2015; Sánchez-Medrano 2018). In western Mexico, most terrestrial alien plant species grow in highly disturbed areas and roadside vegetation; vegetation without recent disturbances contains only a few aliens (Vázquez-García et al. 1995; Cuevas-Guzmán et al. 2004).

In several studies, low and middle elevations have been shown to host most alien plant species (Pauchard et al. 2009; Alexander et al. 2011; Haider et al. 2018). Temperate regions have their maximum number of alien plants at low elevation, whereas subtropical islands have most aliens at middle elevations (Pauchard et al. 2009). These patterns are not only caused by changes in the abiotic conditions along the elevational gradient and the preadaptation of the alien plants, they also depend on the areas of the primary introduction and highest propagule pressure (Pauchard et al. 2006). In most cases, alien species are introduced at low and middle elevations from where they spread towards higher elevations along roads and other dispersal channels. Anthropogenic disturbances, in general, are also higher at low elevations and foster the establishment of aliens (Pauchard et al. 2006; Alexander et al. 2011; Haider et al. 2018).

Very little literature exists on the distribution of alien plant species along the elevational gradient in tropical or subtropical regions, and the results are highly variable. A study from India found the highest numbers of alien plants at the lowest elevations (Kosaka et al. 2010). An investigation in Ecuador showed a hump-shaped distribution (Sandoya et al. 2017). In contrast, in central Argentina, Paiaro et al. (2010) found that the lowest and highest elevations had more alien plant species than middle elevations. In Mexico, this topic has scarcely been broached (Sánchez-González and López-Mata 2005). One study conducted at elevations from 403 to 1930 m in the north-east of Mexico showed no significant correlation between elevation and alien species number; however, abundance was not analysed (Sánchez-Medrano 2018). This lack of publications and the contradictory results highlight the need to improve the understanding of elevations' influence on the distribution of alien species in warmer regions.

We address the following questions in the paper: 1. How does the invasion level of alien roadside plants vary over an elevation gradient? We expect higher richness at low elevations due to more significant anthropogenic disturbances and shorter distances to seaports and major towns as the initial source of aliens. 2. How does the invasion level relate to other environmental variables representing climate, natural and anthropogenic disturbances? We assume the invasion level to be higher at sites closer to main roads and highways, as well as other anthropogenic disturbances such as fire or grazing intensity. Also, soil compaction should influence the abundance of these plants. We limited our study to herbaceous plants as they are much more common and species-rich in Mexico, difficult to manage, and with different dynamics than woody species.

Methods

Study area

The study area was the Sierra de Manantlán and adjoining regions in south-western Jalisco, Mexico (see Fig. 1). This area includes different vegetation types. Coasts have mangroves, temporarily or permanently flooded, and the xerophytic vegetation of the dunes. Dry and humid tropical forests dominate the coastal plain and lower elevations up to 1700 m (Vázquez-García et al. 1995; CONABIO and SEMADET 2017; Rodríguez-Contreras 2017). Cloud forest occurs at elevations between 700 and 2600 m. Forests of *Quercus* and *Pinus* can be found at higher elevations, with *Abies* in protected valley locations and *Cupressus* on ridges and other exposed areas (Vázquez-García et al. 1995; Rodríguez-Contreras 2017). Much of this area is part of the Sierra de Manantlán Biosphere Reserve, which covers an elevational gradient of 400–2850 m (Vázquez-García et al. 1995).

There are two marked seasons, a dry season with only occasional rains and a rainy season of three to four months from June to September. Precipitation patterns differ depending on the exposure: the southern and south-western slopes are windward and

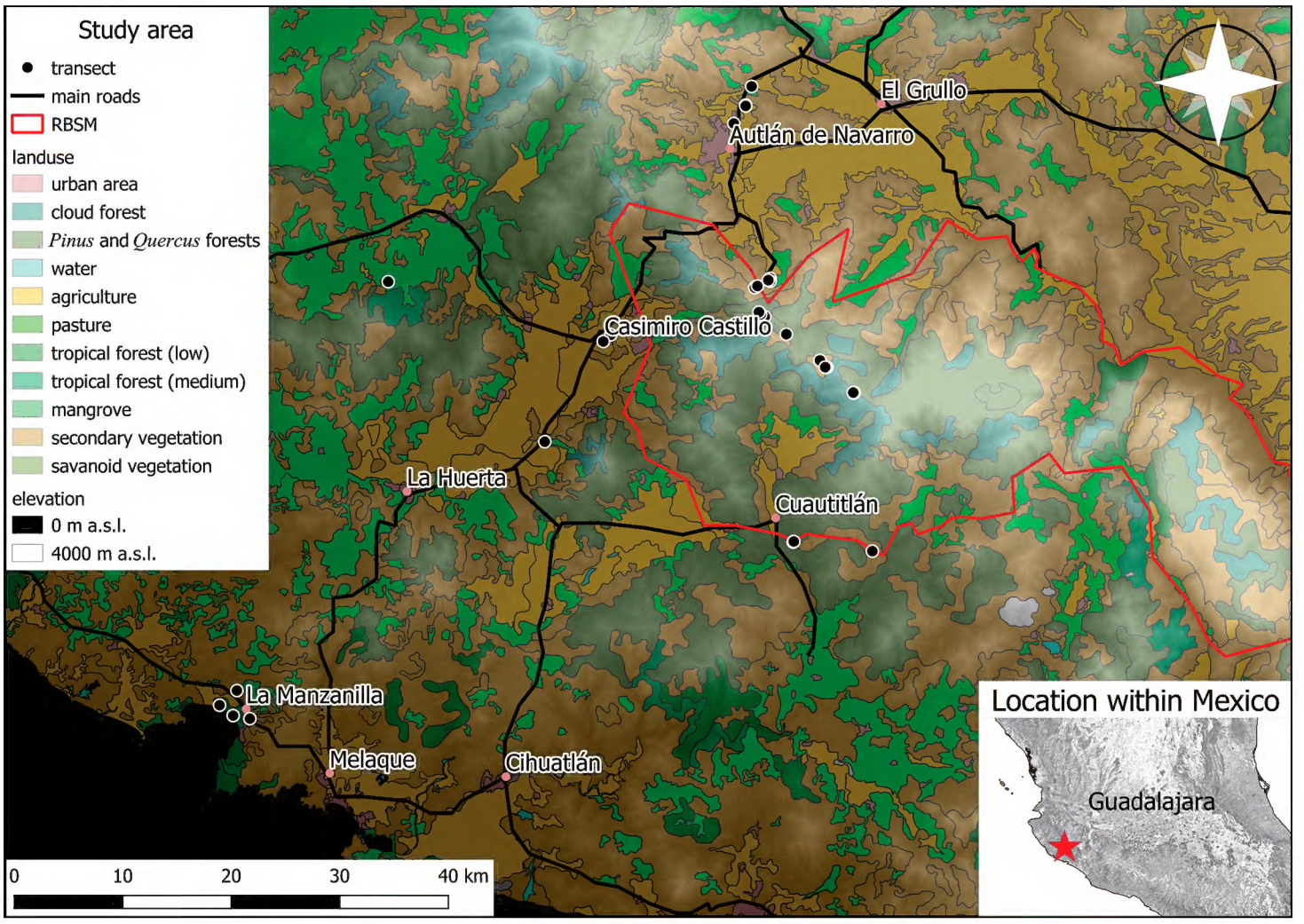

Figure 1. Study area. The biosphere reserve (Reserva de la Biosfera Sierra de Manantlán – RBSM) and its adjoining areas, with the locations of transects and location of the study area in a larger context. Land use and vegetation data from CONABIO (http://www.conabio.gob.mx/informacion/metadata/gis/usv250s6gw.xml?_httpcache=yes&_xsl=/db/metadata/xsl/fgdc_html.xsl&_indent=no).

humid, and the northern and north-eastern slopes of the Sierra are in the rain shadow and have semi-desertic conditions (Vázquez-García et al. 1995).

The plants' intricate distribution patterns result from the above-mentioned climatic factors combined with the geological and evolutionary history. The estimated percentage of endemic species is relatively high: 1% of the plant species in the Sierra de Manantlán is endemic to the Sierra and 3% to the state of Jalisco (Vázquez-García et al. 1995). Humans have influenced the region with varying intensity since the last Ice Age. In the Biosphere Reserve, recent disturbance has been limited to tree cutting and fire; however, in the surrounding areas we also find urban centres, extensive agricultural and ranching areas, and mining in some locations (Jardel-Peláez 1998; Graf-Montero et al. 2003; Jardel-Peláez et al. 2017).

The study area was located in the administrative region Costa-Sur, a geographic region with less than 3% of the population of the state of Jalisco (Aguirre-Jiménez and Castañeda-Huizar 2017). Threats to the biodiversity of the area range from low to high (Curiel and Garibay-Chávez 2017). Agriculture plays an important role in the regional economy; it is one of the areas with the highest productivity of cattle ranching. In recent decades the mining industry has increased and the coast is influenced by tourism (Jardel-Peláez et al. 2017).

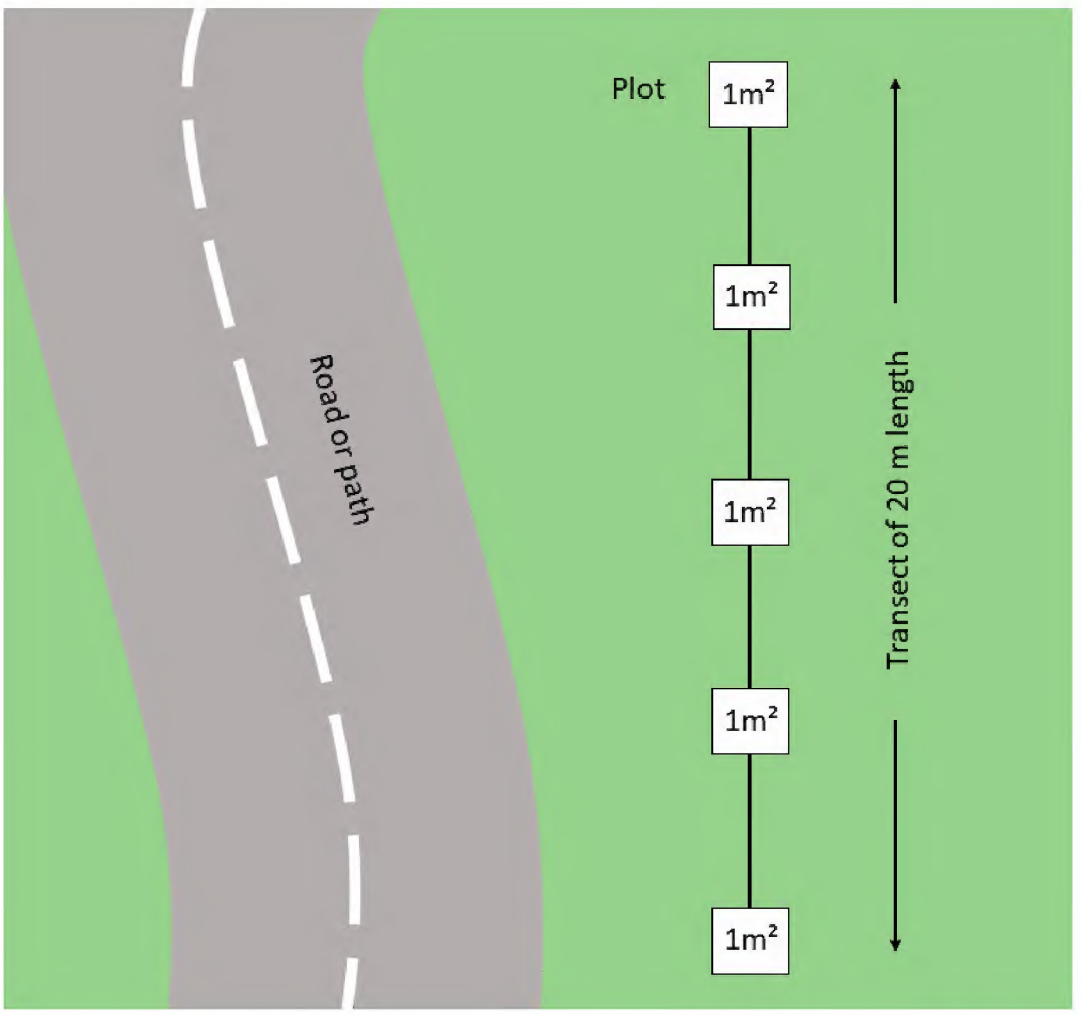

Figure 2. Sampling design, showing the transect location in relation to the road or path with the five 1 m^2 plots.

We worked at sites with ruderal vegetation along an elevational gradient from sea level near the village of La Manzanilla, La Huerta (19°17.78'N, 104°47.67'W) up to elevations just over 2100 m in the Sierra de Manantlán (19°33.82'N, 104°14.95'W). The selection of the locations was preferential and considered the following criteria: elevation, presence of ruderal vegetation, accessibility, and personal security. We searched for appropriate locations from sea level to 2100 m, with an elevational difference of 300 m between them (that is, 0 m, 300 m, 600 m, and so on). We selected ruderal sites with clearly disturbed vegetation near roads, close to abandoned agricultural areas or former pastures (see the map in Fig. 1). We used the concept of Font Quer (1982), which defines the ruderal vegetation as all wild species which form populations in environments altered by human activity, whether or not they are native to the ecosystem; the same definitions were also used by Rzedowski (2006) and Baker (1974).

Data

The data were obtained from 20 m long transects parallel to roads at a distance of 3 to 5 m from the road, to avoid the modified soil near the roadside. We surveyed four to six transects per elevation level, for a total of 37. Some roads were paved or cobbled, but most were dirt roads. Each transect consisted of five plots of 1 m^2 at meter 1, 5, 10, 15, and 20 of the 20 m transect length (see Fig. 2).

All herbaceous species within the 1 m^2 plot were recorded and identified to species level. We collected several individuals of every unknown morpho-species and at least three individuals of every known species for verification. The vouchers were deposited at the ZEA Herbarium of the University of Guadalajara in Autlán de Navarro. The specimens were identified by consulting specialised literature of the regional flora, identification keys, the Tropicos platform of the Missouri Botanical Garden (www.tropicos.org), and the Herbarium ZEA. One of the co-authors (RCG) is an expert on the regional flora.

We collected 500 specimens, with at least three duplicates each, most of which could be identified to 317 species, and one was a new species not yet published. The remaining specimens could only be determined to genus level, resulting in an additional thirty-five morpho-species. To establish which species were alien, we used the publications of Villaseñor and Espinosa-García (2004) and Espinosa-García and Villaseñor (2017) as reference. The list was checked for synonyms.

We documented information on soil and light conditions in the field, and the coordinates with a Garmin eTrex GPS. The slope was measured using a Haga clinometer. Surface stone cover percentage was estimated in four categories, leaf litter depth measured in cm, and the leaf litter cover estimated in percent. For each plot, we measured compaction of the topsoil in kg per cm^2, using a pocket penetrometer from Soil Test Inc. A high topsoil density can be an indicator of disturbances such as grazing or movement of vehicles (Woodward 1996; Rab 2004). Tree cover as a proxy for light availability was measured in percent for each plot using a spherical densiometer Model-A (Robert E. Lemmon Forest Densiometers). Fire and grazing intensity were estimated in five categories each, from none to severe influence as suggested by Olvera et al. (1996).

As mentioned above, not all of our transects were near paved roads with continuous traffic. As a proxy for distance to heavier traffic, we used the distance to paved roads and highways, calculated in QGIS Geographic Information System version 3.10.5, an Open-source Geospatial Foundation Project from The Development Team 2018 using the "distance to nearest hub" function. As reference, we used the data for roads and highways from the year 2012 (Atlas de Caminos y Carreteras del Estado de Jalisco 2012) published by the Government of the State of Jalisco (Datos Abiertos. Gobierno de México, https://datos.gob.mx/).

We also considered the mean temperature and annual precipitation, available at a 30 arc s resolution, the so-called "1 km^2 scale", which is equivalent to around 0.86 km^2 at the equator and less towards the poles. The data were downloaded from the Worldclim database (www.worldclim.org), which includes mean values of the period from 1950 to 2000, interpolated from data from different sources (Hijmans et al. 2005). For every transect we calculated the annual mean temperature and the annual precipitation. The variables were obtained using QGIS for the monthly data and R version 4.0.2 (Ihaka and Gentleman 1996) for the annual data. Suppl. material 5: Table S1 compiles the mean values of all captured variables per transect.

Data analysis

Accumulation curves and the estimated number of species in the pool were calculated for all transects and elevation levels, as quality control, using the functions "specpool" and "specaccum" of the "vegan" package in R (Oksanen et al. 2019). The "specpool" function works with four different equations to extrapolate the species richness in the pool: Chao, bias-corrected Chao, first-order and second-order Jackknife. To discard spatial autocorrelation of species richness patterns, the Moran's I was calculated using the "moran.test" function of the "spdep" package in R (Bivand and Wong 2019).

As a measure of the invasion level, we used the relative alien species richness and relative alien abundance. Both measures consider alien species in relationship with total species (native + alien) richness and abundance of the whole transect (Catford et al. 2012). For the analysis of the relationship of alien invasion level to elevation, generalised linear models were run in R using the "glm" function of the "stats" package (Warton et al. 2016; R Core Team 2020). For total alien and native species richness quasipoisson family was used for the generalised linear model, whereas for the relative alien species richness model the quasibinomial family was selected. For the residuals of all generalised linear models, spatial autocorrelation was tested using the "moran.test" function. Scatter plots and boxplots show the variation of those measures within the elevation levels.

The relation of each environmental variable with alien invasion level, as well as their relative importance and partial dependence, was calculated with the random forest (RF) method. We used the "randomForest" package in R software. RF is a machine learning method based on bagging of classification and regression trees. It is a powerful technique to improve understanding of patterns and processes based on large ecological datasets (Breiman 1996; Liaw and Wiener 2002; Oppel et al. 2009). The program generates a large number of trees, each using a different bootstrap sample of the data, and then searches for the best node split of the tree among a randomly selected subset of predictors. For every bootstrap sample, an unpruned regression tree is grown. The "out-of-bag" (OOB) estimate of error rate is an aggregation of the error rates obtained for each bootstrap iteration (Liaw and Wiener 2002). Results show good performance compared to many other classifiers, and they are robust against overfitting (Breiman 2001; Liaw and Wiener 2002). A pre-selection of variables is not necessary since the RF algorithm works well with continuous and categorical variables and is robust to noise in predictors (Díaz-Uriarte and Alvarez de Andrés 2006; Oppel et al. 2009).

Random forest uses three parameters that have to be defined by the user: the number of trees in the forest, the number of features tried at each node, and the minimum number of data points in each terminal node (Grimm et al. 2008). In some cases, larger numbers of trees obtain more stable results (Díaz-Uriarte and Alvarez de Andrés 2006; Grimm et al. 2008). The number of trees was set to 1000 and the number of variables tried at each node to 4. For the minimum number of data points, we used the default of 5, since higher numbers are only useful for speeding up the calculation time for large datasets.

The relative importance of environmental variables was measured as the increase in mean of error (%IncMSE) of a tree in the forest, when the observed values of this variable were randomly permuted in the OOB samples (Genuer et al. 2010). This variable importance measure is also called permutation importance index. This index and the total decrease of node impurity (IncNodePurity) are the measures used by the "varImp" function for RF variable importance (Breiman 2001). Quantification of variable importance is essential to interpret data and understand underlying phenomena in applied problems, and to rank the variables for modelling (Oppel et al. 2009; Genuer et al. 2010).

Random forest models were run for the relative alien species richness and relative alien abundance; both measures were used at transect (5 m^2) scale. The analysis identified the most important environmental variables (see section "Data"), with the model parameters specified above. Since high correlation between included variables does not affect the results of RF variable importance or model performance in general (Genuer et al. 2010), all environmental variables could be included independently of autocorrelation issues. RF partial dependence plots were printed using the "partialPlot" function to show the partial relation of one variable and the alien species data.

Results

We identified 317 herbaceous species in the transects, of which 285 were natives and 32 aliens (see Suppl. material 6: Table S2). Thirty-five morpho-species could only be identified to genus level and were not included in further analysis. Based on the "specaccum" analysis our sampling effort covered an estimated 75% to 90% of all roadside species in the area. For each elevation level, the proportion of regional species represented in the transects varied between 64% and 88%, depending on the type of analysis (see the "Data analysis" section). Species richness clustering was highly significant for native species with a z-value of .04 (p-value of .0063; Moran's I index). For alien species, richness appeared to be random (z-value of -.06267 and a non-significant p-value of .525).

Elevation was significantly and positively correlated with the richness of native species, though it only explained a small part of the data (p = .007, Fig. 3A). We found no significance for absolute alien species richness (p = .92), though there were more species at lower elevations (Fig. 3B). The generalised linear model for relative alien species richness and relative abundance showed a decrease with elevation, the tendency was significant but the models' estimates were near zero (relative alien species richness: estimate = -.001 and p-value = .028, 35 degrees of freedom, relative alien abundance: estimate = -.001, p-value = .008, 35 degrees of freedom). In natives both relationships were slightly positive and significant. Spatial autocorrelation could be rejected due to high p-values at the Moran's I test of all generalised linear models. Scatter and boxplots (Fig. 3C,D) show the relative species richness per transect along the elevation gradient and the variation within the elevation levels for alien species.

For relative alien species richness, the most influential variables were (i) the distance to highways, (ii) the elevation and (iii) tree cover, followed by (iv) the annual mean temperature, (v) the slope and (vi) distance to roads (Fig. 4). The relation shown

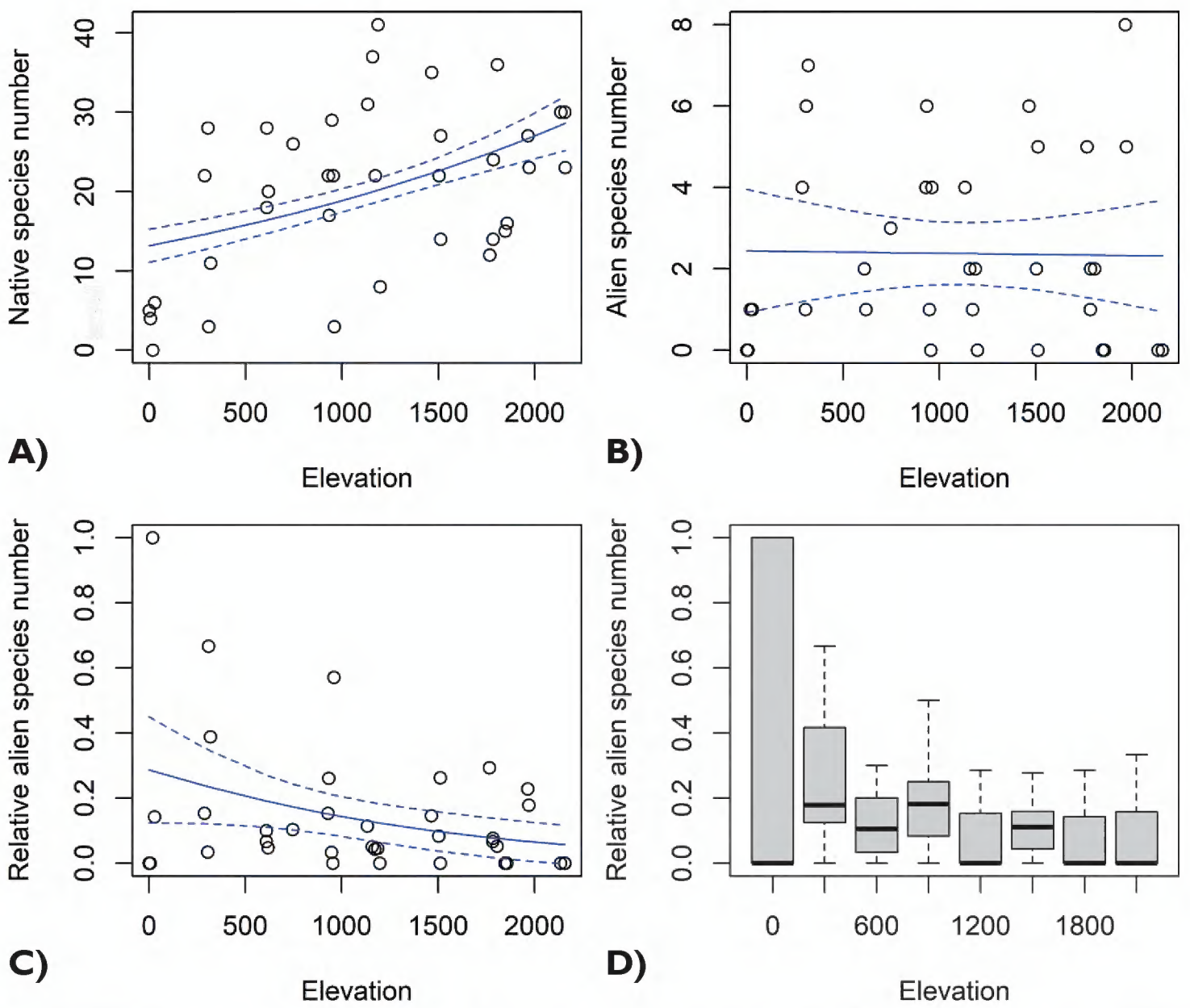

Figure 3. Absolute and relative species richness over elevation in m. Blue lines showing glm predicted values with the 95% confidence interval **A** total species richness of native herbaceous plants over elevation. Glm coefficient = .0003, p-value = .007, 35 degrees of freedom **B** total species richness of alien herbaceous plants over elevation. Glm coefficient = -2.386e-05, p-value = .92, 36 degrees of freedom **C** relative species richness of alien herbaceous plants over the elevation. Glm coefficient = -.0009, p-value = .0276, 35 degrees of freedom **D** relative species richness of alien herbaceous plants, represented by boxplots for each elevation level. They show the median per transect (5 m^2), third and first quartile and extreme values.

by the partial dependence plots (Fig. 5A–C) of relative species richness to distance to highways was non-linear positive, the relation to elevation was also positive, whereas the relation to tree cover was slightly U-shaped. Both random forest models were significant with low mean squared errors (mean of squared residuals) for relative alien species richness and relative alien abundance. But the variance explained by the models was very low in both cases (see Table 1).

The most important variables for the relative abundance of alien species were (i) the annual mean temperature, (ii) elevation, and (iii) the leaf litter depth, followed by (iv) slope, (v) the distance to highways, and (vi) the tree cover (Suppl. material 1: Fig. S1). The relation of relative alien species abundance to the mean temperature was negative, the relation to elevation was positive and the relation to leaf litter depth was also negative (see Suppl. material 2: Fig. S2, Suppl. material 3: Fig. S3, Suppl. material 4: Fig. S4).

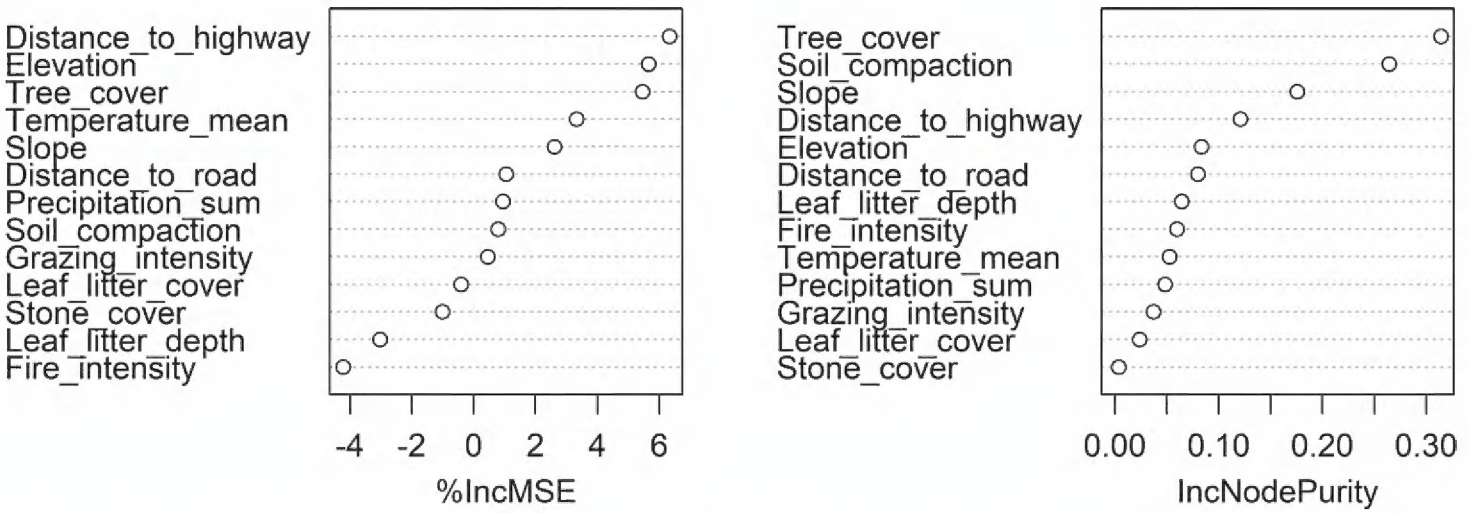

Figure 4. Variable importance for relative alien species richness according to the random forest calculations. The figure shows the increase in mean of the error (%IncMSE), also called permutation importance index, on the left side; and the total decrease of node impurity (IncNodePurity) on the right side (distance to highways in m, calculated from open data Jalisco; elevation above sea level in m; tree cover measured per plot; mean annual temperature, obtained from Worldclim data; slope of the transect measured in %; distance to paved roads in m, calculated from open data Jalisco; mean annual precipitation sum, obtained from Worldclim data; soil compaction, measured in kg/m^2; grazing intensity estimated as an index from 0/none to 5/severe; leaf litter cover measured in percent of the plot area; stone cover measured in percent of the plot area; leaf litter depth in cm measured in the field; fire intensity estimated as an index from 0/none to 5/severe).

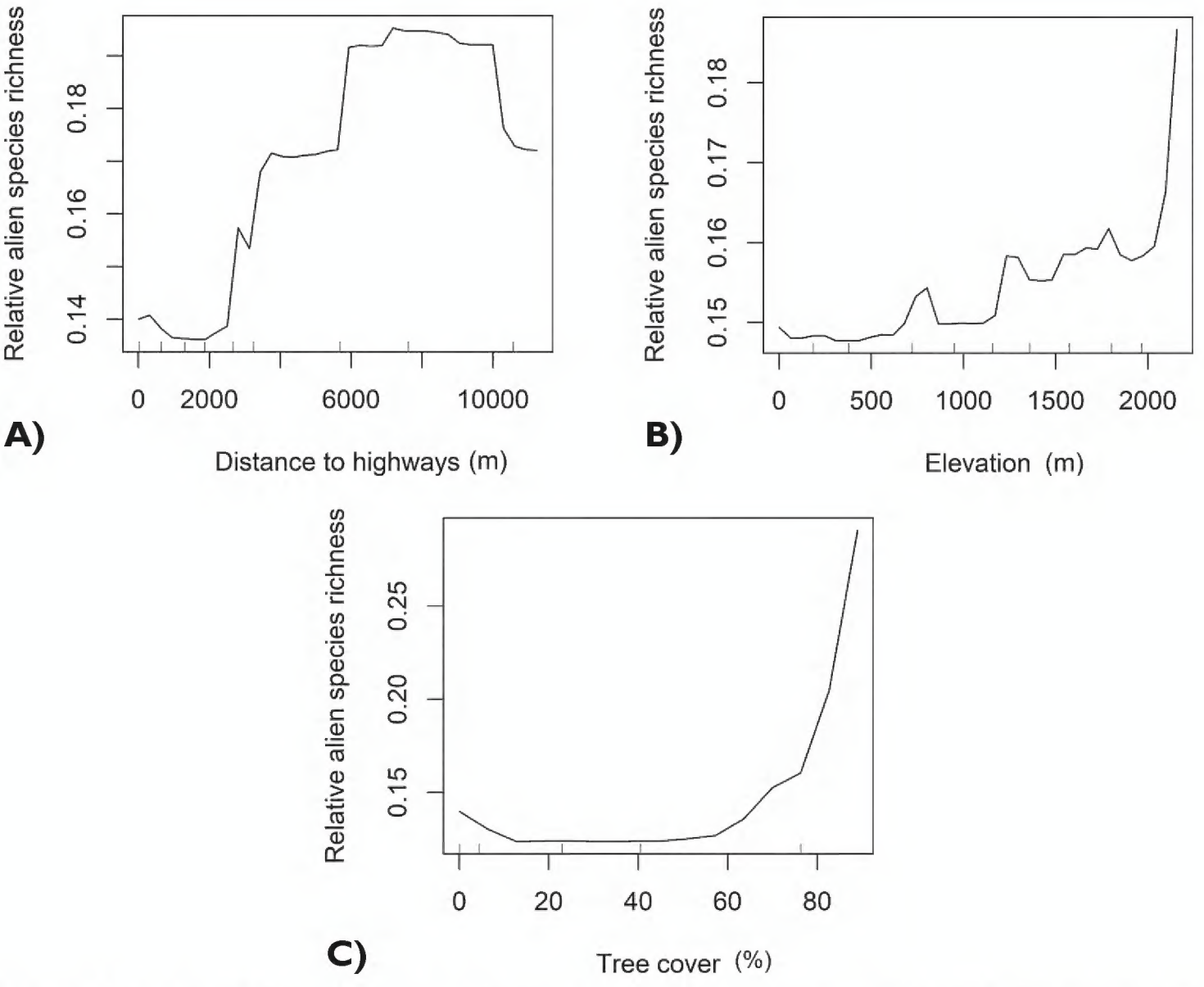

Figure 5. Relation of the relative alien species richness to the most important variables. Partial dependence plots for the distance to highways (**A**), the elevation (**B**) and tree cover (**C**).

Table 1. Random forest model performance for relative species richness and relative abundance of alien species. It shows the variance in % explained by the model and the mean of squared residuals as measure of model performance is shown.

Model	Variance explained by the model (%)	Mean of squared residuals
Relative species richness	-9.83	.048
Relative abundance	-8.06	.065

Discussion

The 317 identified species were the equivalent of approximately 12% of the total vascular flora of the Sierra de Manantlán (Vázquez-García et al. 1995). This proportion matches earlier publications on the weed vegetation of Mexico, which show that 10–12% of the Mexican flora are agrestal or ruderal weeds (Espinosa-García et al. 2004b; Vibrans 2016).

The 32 alien species we identified constitute 10% of the herbaceous flora of the samples. This share is low compared to other regions in the country, where the mean percentage of alien species in weedy vegetation is around 20% (Espinosa-García et al. 2004a, b; Vibrans 2016). The maize field weed vegetation of Puebla and Tlaxcala in central Mexico had 16.4% alien species (Vibrans 1998). A share of 26% of 125 ruderal plants in the urban area of Malinalco in the State of Mexico were aliens (Martínez-De La Cruz et al. 2015). In a study in Mexico City during the 1990s, 37% of 256 ruderal weed species had been introduced from other continents (Vibrans 1998).

The results of the studies are consistent with the remarkably low number of alien plant species that Mexico has in general when seen in a global context, and despite a long history of commercial exchange with Europe, other parts of North America, and Asia (Philippines). The low proportion may be related to the long history of human disturbance and agriculture in the Mesoamerican cultural region. This history promoted the development of native weed communities, which in turn may prevent an excessive invasion of alien plants (Vibrans 1998; Rejmánek et al. 2005; Kühn and Klotz 2007; Vibrans 2016). With further study of the local natural history, we might be able to improve our understanding of this relatively low number of aliens.

Though more alien species were recorded at lower elevations, no statistically clear relationship was found. Spatial autocorrelation could be rejected for all models. However, the tendency partly reflects what the literature has shown for other cases: there are more alien species at lower elevations, mainly due to lower human population densities at high elevations (Alexander et al. 2011; Pollnac et al. 2012; Otto et al. 2014; Haider et al. 2018), but confounding factors may complicate the relationship. In contrast, native species richness of herbaceous plants tends to rise with elevation (Rzedowski and Calderon de Rzedowski 1989), a tendency we also found. Another study in north-eastern Mexico (Sánchez-Medrano 2018) found a similar tendency, but also not significant. The absence of aliens close to the coast might be related to the environmental conditions, where only highly specialised species, such as mangrove

species or halophytes can survive (Vázquez-García et al. 1995; CONABIO and SEMADET 2017; Rodríguez-Contreras 2017).

Relative alien species richness and abundance patterns were closely related, which means that dominant species react in the same way to environmental variables as less dominant species. The RF models for relative species richness and abundance had a low mean of squared residuals, indicating a good performance. But low (negative) variances explained by the models showed that variances of the species data could not be explained by the environmental variables.

The distance to highways was the most significant variable for relative species richness. Up to a distance of around 1 km the relation was negative. After this it was, unexpectedly, mainly positive and contradicted our hypothesis as well as previous literature (Otto et al. 2014; Haider et al. 2018; McDougall et al. 2018). This variable not only represents the distance to major transport routes where aliens are moved by traffic and can establish first (Kowarik and von der Lippe 2007), but also the distance to human-influenced areas in general. We don't yet have an explanation for this curious phenomenon.

The results from the generalised linear models and the random forest models were contradictory, but in both cases the relations were not very strong. The generalised linear models showed a weak negative relation of the invasion level to elevation. For both random forest models the invasion level was positively related to elevation and negatively to temperature. In other studies alien species richness (not relative species richness) decreased with increasing elevation (Pollnac et al. 2012; Otto et al. 2014; Haider et al. 2018).

McDougall et al. (2018) showed that world-wide species richness patterns vary in function of elevation, depending on certain traits. Perennial species showed an increase with elevation in the roadside vegetation, annual species decreased, but the total of ruderal species richness did not change over elevation (McDougall et al. 2018). In our case, classification into annuals / perennials or ruderal / non-ruderal was not possible because of lack of published information. However, the data suggest intriguing elevational patterns related to biological traits may exist.

The relationship between tree cover and leaf litter depth seems to contradict each other, as both can be considered indicators for disturbance. For the relative species richness model, tree cover was the third most important variable, with a positive relation. For relative abundance leaf litter depth was at the third position, showing a negative relation. However, this contradiction may be explained by some herbaceous alien species requiring sufficient light to grow, although they may germinate below leaf litter (Veldman and Putz 2010).

Our results show that relative alien species richness and abundance were not strongly related to any of the environmental variables included in this study. Different factors may cause this seemingly random distribution. Previous studies show that the influence of environmental variables on the invasion process varies with the ecosystem (Lonsdale 1999; Rejmánek et al. 2005; Richardson and Pyšek 2006; Kühn

and Klotz 2007). The number of species and abundance of natives also influences the results, as we are working with relative values. At the 1 m^2 scale higher native species richness can be expected to reduce the probability of finding alien species; at larger scales this relation is inverted (Kühn and Klotz 2007; Pauchard and Shea 2016). As we focused only on roadside vegetation which represent dispersion channels for primary invasion, we suggest that the alien species have not yet concluded the phase of the primary introduction (McDougall et al. 2018).

The conversion from traditional to modern agriculture and urbanisation has caused land-use change on a large scale (Jardel-Peláez 1998; Instituto Nacional de Ecología 2000; Graf-Montero et al. 2003). This change, particularly from agriculture to cattle ranching, has taken place mainly in the last five decades. With this the introduction and propagation of new alien species have risen significantly (Villaseñor and Espinosa-García 2004; Vibrans 2016; Ramirez-Albores et al. 2019). This period is relatively short for the introduced species to establish in their new habitats, and to expand significantly and reach the potential maximum distribution that reflect their biology (Kowarik and von der Lippe 2007; McDougall et al. 2018). Many alien species are known to have a lag-phase during the first decades after introduction, where they remain at low numbers and in few localities before their populations start to increase (Aikio et al. 2010). Therefore, the present-day distribution might represent the lag-phase distribution and thus depend mainly on the location and intensity of the initial introduction. To confirm this, further studies should include similar regions in central and western Mexico. Species records from herbarium data could be used to analyse the temporal trends of the invasion, although sampling biases and other potential errors could hamper this (Aikio et al. 2010).

Many African grasses have been planted on large areas as forage for cattle, but only in the last 100 years, and often even more recently (Rzedowski 1990; Williams and Baruch 2000). The intensity of the introduction or propagule pressure is a crucial factor for alien plant distribution patterns. It is difficult to measure and was not included in this study (Richardson and Pyšek 2006). Even though initial introductions of all alien plants are directly linked to human activities (Reichard and White 2001; Kowarik 2005; Kowarik and von der Lippe 2007), the number, distribution, and frequency of repeated introductions can vary considerably.

For eradication success, the size of the distribution area of the alien species and the time since the initial introduction are highly relevant (Coulston 2004; Mack and Lonsdale 2004; West 2004; Gardener et al. 2009; Kettenring and Adams 2011; Pluess et al. 2012). In the case of western Mexico with low total numbers of alien species, which have been introduced recently and not yet expanded, targeted management could make containment possible (Bruce and Johnson 2014). The large number of native weedy plants may help with management. After local eradication of alien species, it is important to re-establish the native flora, and these strong native competitors could be used to initiate appropriate succession (Kettenring and Adams 2011).

Conclusion

Western Mexico has relatively few alien herbaceous roadside species. They can be found mainly at lower elevations but not directly at the coast. This pattern was expected as introductions occur mainly at lower elevations, where a large part of the land is converted to agricultural land and other uses. Although the relationship was statistically significant, low values of the estimates showed a weak relationship. The result may be related to another finding: the lack of clustering of alien species richness. Both results could be attributed to the fact that most introductions have been relatively recent. The region's alien plant species have probably not yet expanded sufficiently to show clear distribution patterns. For comparison and in order to confirm this assumption, similar studies would have to be conducted in central and western Mexico. It would be interesting to repeat the study in the future and include further plots in the natural adjacent vegetation to see how the situation develops. In the future, and especially if further introductions are not limited to a minimum, and no targeted management is applied, the number and abundance of alien herbaceous plant species will probably increase. This situation can be viewed as an opportunity to prevent the expansion of introduced species and prevent large-scale invasions through management. Identifying the potential invaders and their potential distribution helps to concentrate management strategies on threatened areas.

Acknowledgements

This study was conducted in the context of the Doctorate Program in Sciences in Biosystematics, Ecology, and Management of Natural and Agricultural Resources (BEMARENA) of the Universidad de Guadalajara, Mexico. The Consejo Nacional de Ciencia y Tecnología (CONACyT), Mexico, funded the research through a doctoral thesis grant to the first author. We received financial support from the University of Guadalajara through the program Fortalecimiento a la investigación, provided by the Coordinación de Investigación, Posgrado y Vinculación. Members of the Laboratory of the Botany Department at the Centro Universitario de la Costa Sur of the Universidad de Guadalajara helped with the field work and species identification. For the data analysis, we were assisted by the members of the Laboratory for Climatology and Remote Sensing (LCRS) of the Philipps University of Marburg, Germany. The authors declare that no competing interests exist.

References

Aguirre-Jiménez AA, Castañeda-Huizar P (2017) Población. In: La biodiversidad en Jalisco. Estudio de Estado. Vol 1. CONABIO, Mexico, 81–97.

Aikio S, Duncan RP, Hulme PE (2010) Lag-phases in alien plant invasions: separating the facts from the artefacts. Oikos 119: 370–378. https://doi.org/10.1111/j.1600-0706.2009.17963.x

Alexander JM, Kueffer C, Daehler CC, Edwards PJ, Pauchard A, Seipel T, MIREN Consortium (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. PNAS 108: 656–661. https://doi.org/10.1073/pnas.1013136108

Baker H (1974) The evolution of weeds. Annual Review of Ecology and Systematics 5: 1–24. https://doi.org/10.1146/annurev.es.05.110174.000245

Bivand R, Wong DWS (2019) Comparing implementations of global and local indicators of spatial association. TEST 27: 716–748. https://doi.org/10.1007/s11749-018-0599-x

Breiman L (1996) Bagging predictors. Machine Learning 24: 123–140. https://doi.org/10.1007/BF00058655

Breiman L (2001) Random Forests. Machine Learning 45: 5–32. https://doi.org/10.1023/A:1010933404324

Bruce B, Johnson S (2014) Invasive alien plant management. CAB Reviews 9: 1–13. https://doi.org/10.1079/PAVSNNR20149037

Catford JA, Vesk PA, Richardson DM, Pyšek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. Global Change Biology 18: 44–62. https://doi.org/10.1111/j.1365-2486.2011.02549.x

CONABIO, SEMADET (2017) La biodiversidad en Jalisco. Estudio de Estado. Vol. II. (Ciudad de México): 1–400.

Coulston GJ (2004) Control of invasive plants on the Poor Knights Islands, New Zealand. In: Veitch CR, Clout MN (Eds) Turning the tide: the eradication of invasive species, 2002. IUCN SSC Invasive Species Specialist Group (Cambridge), 79–84.

Cuevas-Guzmán R, Koch S, García-Moya E, Núñez-López NM, Jardel-Peláez EJ (2004) Flora vascular de la Estación Científica las Joyas. Universidad de Guadalajara (Guadalajara), 294 pp.

Curiel A, Garibay-Chávez MG (2017) Amenazas de la biodiversidad. In: La biodiversidad en Jalisco. Estudio de Estado. Vol 1. CONABIO, Mexico, 251–262.

Díaz-Uriarte R, Alvarez de Andrés S (2006) Gene selection and classification of microarray data using random forest. BMC Bioinformatics 7: 1–13. https://doi.org/10.1186/1471-2105-7-3

Espinosa-García FJ (2009) Invasive weeds in Mexico: Overview of awareness, management and legal aspects. In: Darbyshire SJ, Prasad R (Eds) Weeds Across Borders. Alberta Invasive Plant Council (Alberta), May 2008, 17–29.

Espinosa-García FJ, Villaseñor JL (2017) Biodiversity, distribution, ecology and management of non-native weeds in Mexico: a review. Revista Mexicana de Biodiversidad 88: 76–96. https://doi.org/10.1016/j.rmb.2017.10.010

Espinosa-García FJ, Vibrans H, Villaseñor JL (2004a) Geographical patterns in native and exotic weeds of Mexico. Weed Technology 18: 1552–1558. https://doi.org/10.1614/0890-037X(2004)018[1552:GPINAE]2.0.CO;2

Espinosa-García FJ, Villaseñor JL, Vibrans H (2004b) The rich generally get richer, but there are exceptions: Correlations between species richness of native plant species and alien weeds in Mexico. Diversity and Distributions 10: 399–407. https://doi.org/10.1111/j.1366-9516.2004.00099.x

Font Quer P (1982) Diccionario de Botánica. Editorial Labor, S.A. Barcelona, España.

Gardener M, Atkinson R, Renter J (2009) Eradications and people: Lessons from the plant eradication program in Galapagos. Restoration Ecology 18: 1–10. https://doi.org/10.1111/j.1526-100X.2009.00614.x

Genuer R, Poggi J-M, Tuleau-Malot C (2010) Variable selection using Random Forests. Pattern Recognition Letters 31: 2225–2236. https://doi.org/10.1016/j.patrec.2010.03.014

Graf-Montero S, Santana CE, Jardel-Peláez EJ, Gómez M, García-Ruvalcaba S (2003) La reserva de la biosfera Sierra de Manantlán, México. In: Desarrollo de capacidades para el manejo de áreas protegidas: América Latina y el Caribe, Parque Nacional Huascarán (Perú), August 2002: 135–152.

Grimm R, Behrens T, Märker M, Elsenbeer H (2008) Soil organic carbon concentrations and stocks on Barro Colorado Island – Digital soil mapping using Random Forests analysis. Geoderma 146: 102–113. https://doi.org/10.1016/j.geoderma.2008.05.008

Haider S, Kueffer C, Bruelheide H, Seipel T, Alexander JM, Rew LJ, Cavieres LA, Mcdougall KL, Milbau A (2018) Mountain roads and non-native species modify elevational patterns of plant diversity. Global Ecology and Biogeography 27: 667–678. https://doi.org/10.1111/geb.12727

Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978. https://doi.org/10.1002/joc.1276

Ihaka R, Gentleman R (1996) R: A language for data analysis and graphics. Journal of Computational and Graphical Statistics 5: 299–314. https://doi.org/10.2307/1390807

Instituto Nacional de Ecología (2000) Programa de manejo reserva de la biosfera Sierra de Manantlán, México, 204 pp.

Jardel-Peláez EJ (1998) Efectos ecológicos y sociales de la explotación maderera de los bosques de la Sierra de Manantlán. In: Ávila R, Emphoux JP, Gastélum LG, Ramírez O, Schöndube S, Valdez F (Eds) El Occidente de México: arqueología, historia y medio ambiente. Perspectivas regionales. Universidad de Guadalajara / Instituto Francés de Investigación Científica para el Desarrollo en Cooperación, ORSTOM (Guadalajara), 231–251.

Jardel-Peláez EJ, Santana E, Graf SH, Hernández-López L, Valencia C, González-Franco R, Meiners M (2017) Conservación y restauración. In: La biodiversidad en Jalisco. Estudio de Estado. Vol 1. CONABIO, Mexico, 275–316.

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. Journal of Applied Ecology 48: 970–979. https://doi.org/10.1111/j.1365-2664.2011.01979.x

Kosaka Y, Saikia B, Mingki T, Tag H, Riba T, Ando K (2010) Roadside distribution patterns of invasive alien plants along an altitudinal gradient in Arunachal. Mountain Research and Development 30: 252–258. https://doi.org/10.1659/MRD-JOURNAL-D-10-00036.1

Kowarik I (2005) Urban ornamentals escaped from cultivation. In: Gressel J (Ed.) Crop Ferality and Volunteerism. CRP Press (Boca Raton): 97–121. https://doi.org/10.1201/9781420037999.ch7

Kowarik I, von der Lippe M (2007) Pathways in plant invasions. In: Nentwig W (Ed.) Biological Invasions: why it Matters. Springer International Publishing (Berlin): 29–48. https://doi.org/10.1007/978-3-540-36920-2_1

Kühn I, Klotz S (2007) From ecosystem invasibility to local, regional and global patterns of invasive species. In: Nentwig W (Ed.) Biological Invasions. Springer International Publishing (Berlin): 181–196. https://doi.org/10.1007/978-3-540-36920-2_1

Liaw A, Wiener M (2002) Classification and regression by randomForest. R News 2: 18–22.
Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80: 1522–1536. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2
Mack R, Lonsdale W (2004) Eradicating invasive plants. hard-won lessons for islands. In: Veitch CR, Clout MN (Eds) Turning the tide: the eradication of invasive species, 2002. IUCN SSC Invasive Species Specialist Group (Cambridge): 165–172.
Martínez-De La Cruz I, Vibrans H, Lozada-Pérez L, Romero-Manzanares A, Aguilera-Gómez LI, Rivas-Manzano IV (2015) Plantas ruderales del área urbana de Malinalco, Estado de México, México. Botanical Sciences 93: 907–919. https://doi.org/10.17129/botsci.213
McDougall KL, Lembrechts J, Rew LJ, Haider S, Wright GT, Alexander JM (2018) Running off the road: roadside non-native plants invading mountain vegetation. Biological Invasions 20: 3461–3473. https://doi.org/10.1007/s10530-018-1787-z
Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) vegan: Community ecology package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan
Olvera-Vargas M, Moreno-Gómez S, Figueroa-Rangel B (1996) Sitios permanentes para la investigación silvícola. Universidad de Guadalajara (Guadalajara): 1–61.
Oppel S, Strobl C, Huettmann F (2009) Alternative methods to quantify variable importance in ecology. Technical Report Number 65. University of Munich, 1–6.
Otto R, Arteaga MA, Delgado JD, Arévalo JR, Blandino C, Fernández-Palacios JM (2014) Road edge effect and elevation patterns of native and alien plants on an oceanic island (Tenerife, Canary Islands). Folia Geobotanica 49: 65–82. https://doi.org/10.1007/s12224-013-9159-z
Paiaro V, Cabido M, Pucheta E (2010) Altitudinal distribution of native and alien plant species in roadside communities from central Argentina. Austral Ecology 36: 176–184. https://doi.org/10.1111/j.1442-9993.2010.02134.x
Pauchard A, Shea K (2006) Integrating the study of non-native plant invasions across spatial scales. Biological Invasions 8: 399–413. https://doi.org/10.1007/s10530-005-6419-8
Pauchard A, Kueffer H, Dietz H, Daehler CC, Alexander J, Edwards PJ, Arévalo JR, Cavieres LA, Guisan A, Haider S, Jakobs G, McDougal K, Millar CI, Naylor BJ, Parks CG, Rew LJ, Seipel T (2009) Ain't no mountain high enough: plant invasions reaching new elevations. Frontiers in Ecology and the Environment 7: 479–486. https://doi.org/10.1890/080072
Pluess T, Cannon R, Jarosik V, Pergl J, Pyšek P, Bacher S (2012) When are eradication campaigns successful? A test of common assumptions. Biological Invasions 14: 1365–1378. https://doi.org/10.1007/s10530-011-0160-2
Pollnac F, Seipel T, Repath C, Rew LJ (2012) Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem. Biological Invasions 14: 1753–1763. https://doi.org/10.1007/s10530-012-0188-y
R Core Team (2020) R: A language and environmental for statistical computing. R Foundation for Statistical Computing, Vienna. https://www-R-project.org/
Rab MA (2004) Recovery of soil physical properties from compaction and soil profile disturbance caused by logging of native forest in Victorian Central Highlands, Australia. Forest Ecology and Management 191: 329–340. https://doi.org/10.1016/j.foreco.2003.12.010

Ramírez-Albores JE, Badano EI, Flores J, Flores-Flores JL, Yáñez-Espinosa L (2019) Scientific literature on invasive alien species in an megadiverse country: Advances and Challenges in Mexico. NeoBiota 127: 113–127. https://doi.org/10.3897/neobiota.48.36201

Reichard S, White P (2001) Horticulture as pathways of plant introductions in the United States. BioScience 51: 103–113. https://doi.org/10.1641/0006-3568(2001)051[0103:HAAPOI]2.0.CO;2

Rejmánek M, Richardson DM, Pyšek P (2005) Plant invasions and invasibility of plant communities. In: van der Maarel E (Ed.) Vegetation Ecology. Blackwell (Oxford): 332–355.

Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30: 409–431. https://doi.org/10.1191/0309133306pp490pr

Rodríguez-Contreras A (2017) Ecorregiones terrestres. In: CONABIO, SEMADET (Eds) La biodiversidad en Jalisco. Estudio de Estado. Vol. II (México), 27–60.

Rzedowski J, Calderon de Rzedowski G (1989) Sinopsis numérica de la flora fanerogamica del valle de México. Acta Botanica Mexicana 8: 15–30. https://doi.org/10.21829/abm8.1989.583

Rzedowski J, Calderon de Rzedowski G (1990) Nota sobre el elemento africano en la flora adventicia de México. Acta Botanica Mexicana 12: 21–24. https://doi.org/10.21829/abm12.1990.602

Rzedowski J (2006) Vegetación de México. 1st digital edn. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Mexico), 504 pp.

Sánchez-González A, López-Mata L (2005) Plant species richness and diversity along an altitudinal gradient in the Sierra Nevada, Mexico. Diversity and Distributions 11: 567–575. https://doi.org/10.1111/j.1366-9516.2005.00186.x

Sánchez-Medrano FZ (2018) Distribución de especies de plantas nativas y exóticas al lado de caminos a lo largo de un gradiente altitudinal en el noreste de México. Master Thesis. Universidad Autónoma de Nuevo León (Linares).

Sandoya V, Pauchard A, Cavieres L (2017) Natives and non-natives plants show different responses to elevation and disturbance on tropical high Andes of Ecuador. Ecology and Evolution 7: 7909–7919. https://doi.org/10.1002/ece3.3270

Trejo I, Dirzo R (2002) Floristic diversity of Mexican seasonally dry tropical forests. Biodiversity & Conservation 11: 2048–2063. https://doi.org/10.1023/A:1020876316013

van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, Kreft H, Weigelt P, Kartesz J, Nishino M, Antonova LA, Barcelona JF, Cabezas FJ, Cárdenas D, Cárdenas-Toro J, Castaño N, Chacón E, Chatelain C, Ebel AL, Figueiredo E, Fuentes N, Groom QJ, Henderson L, Inderjit, Kupriyanov A, Masciadri S, Meerman J, Morozova O, Moser D, Nickrent DL, Patzelt A, Pelser PB, Baptiste MP, Poopath M, Schulze M, Seebens H, Shu WS, Thomas J, Velayos M, Wieringa JJ, Pyšek P (2015) Global exchange and accumulation of non-native plants. Nature 525: 100–103. https://doi.org/10.1038/nature14910

Vázquez-García JA, Cuevas-Guzmán R, Cochrane TS, Iltis HH, Santana MFJ, Guzmán HL (1995) Flora de Manantlán. Botanical Research Institute of Texas (Forth Worth), 315 pp.

Veldman JW, Putz FE (2010) Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. Biotropica 42: 697–703. https://doi.org/10.1111/j.1744-7429.2010.00647.x

Vibrans H (1998) Native maize field weed communities in south-central Mexico. Weed Research 38: 153–166. https://doi.org/10.1046/j.1365-3180.1998.00082.x

Vibrans H (2016) Ethnobotany of Mexican weeds. In: Lira R, Casas A, Blancas J (Eds) Ethnobotany of Mexico. Springer Science + Business Media (New York), 287–317. https://doi.org/10.1007/978-1-4614-6669-7_12

Villaseñor JL, Espinosa-García FJ (2004) The alien flower plants of Mexico. Diversity and Distributions 10: 113–123. https://doi.org/10.1111/j.1366-9516.2004.00059.x

Warton D, Lyons M, Stoklosa J, Ives AR (2016) Three points to consider when choosing a LM or GLM test for count data. Methods in Ecology and Evolution 7: 882–890. https://doi.org/10.1111/2041-210X.12552

West C (2004) Eradication of alien plants on Raoul Island, Kermadec Islands, New Zealand. In Veitch CR, Clout MN (Eds) Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group (Cambridge), 365–373.

Williams D, Baruch Z (2000) African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. Biological Invasions 2: 123–140. https://doi.org/10.1023/A:1010040524588

Woodward CL (1996) Soil compaction and topsoil removal effects on soil properties and seedling growth in Amazonian Ecuador. Forest Ecology and Management 82: 197–209. https://doi.org/10.1016/0378-1127(95)03667-9

Supplementary material 1

Figure S1

Authors: Isabel Pérez-Postigo

Data type: png image

Explanation note: Variable importance for relative abundance of alien species according to the random forest calculations. The figure shows the increase in mean of the error (%IncMSE), also called permutation importance index, on the left side; and the total decrease of node impurity (IncNodePurity) on the right side. (distance to highways in m, calculated from open data Jalisco; elevation above sea level in m; tree cover measured per plot; mean annual temperature, obtained from Worldclim data; slope of the transect measured in %; distance to paved roads in m, calculated from open data Jalisco; mean annual precipitation sum, obtained from Worldclim data; soil compaction, measured in kg/m^2; grazing intensity estimated as an index from 0/none to 5/severe; leaf litter cover measured in percent of the plot area; stone cover measured in percent of the plot area; leaf litter depth in cm measured in the field; fire intensity estimated as an index from 0/none to 5/severe).

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Supplementary material 2

Figure S2
Authors: Isabel Pérez-Postigo
Data type: png image
Explanation note: Relation of the relative abundance of alien species with the most important variables. Partial dependence plot for the annual mean temperature.
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Supplementary material 3

Figure S3
Authors: Isabel Pérez-Postigo
Data type: png image
Explanation note: Relation of the relative abundance of alien species with the most important variables. Partial dependence plot for elevation.
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Supplementary material 4

Figure S4
Authors: Isabel Pérez-Postigo
Data type: png image
Explanation note: Relation of the relative abundance of alien species with the most important variables. Partial dependence plot for leaf litter depth.
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Supplementary material 5

Table S1
Authors: Isabel Pérez-Postigo
Data type: excel table
Explanation note: Mean values of the environmental variables per transect.
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Link: https://doi.org/10.3897/neobiota.65.67192.suppl5

Supplementary material 6

Table S2
Authors: Isabel Pérez-Postigo
Data type: excel table
Explanation note: Alien herbaceous species registered in the study area.
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Link: https://doi.org/10.3897/neobiota.65.67192.suppl6